How warm was Britain during the Last Interglacial? A critical review of Ipswichian (MIS 5e) palaeotemperature reconstructions

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Abstract

The Last Interglacial (LIG, equivalent to marine isotope stage (MIS) 5e) was a period of enhanced global warmth, with potential significance for understanding future climate warming. It has long been proposed that the LIG in Britain (the Ipswichian Interglacial) was significantly warmer than present, based on the occurrence of fossils of extant thermophilous plant and animal species intolerant of the current climate. Here, we review the evidence for palaeotemperatures that can be derived from such fossil taxa (beetles, ostracods, plant macrofossils and herpetiles) in order to assess the level of warmth that Britain experienced during the LIG. Quantified palaeotemperature reconstructions generated for eight British sequences indicate that the LIG was likely to have been warmer than the present but at only one site (Trafalgar Square) is there strong evidence for climates that were significantly warmer than those experienced curing the Holocene. Consequently, whilst there is evidence to support the idea that the thermal regime of the LIG in Britain was different from that of the

Holocene this evidence is restricted to a single site. The paper concludes by discussing the thermal regime of the LIG in Britain in the context of its role as an analogue for future warming in the 21st century and beyond.

Last Interglacial, MIS 5e, future warming, Ipswichian, palaeotemperatures

Introduction

The Last Interglacial (LIG, marine oxygen isotope stage (MIS) 5e) is often considered a partial analogue for the warming scenarios predicted for the Earth from 2100 onwards. This comparison is based on evidence that MIS 5e experienced a level of warming, relative to the present day, that may also be expected under a number of IPCC emissions scenarios (Kopp et al., 2009; Turney and Jones, 2010; Masson-Delmotte et al., 2006, 2010; Lunt et al., 2013; NEEM, 2013). It has been estimated that global mean surface temperatures during the thermal maximum of MIS 5e were 2^{o}C greater than present (Masson-Delmotte et al., 2006, 2010; Lunt et al., 2013); the impact of this warmth on the Earth system has implications for understanding future change, since it has been suggested that parts of the Greenland and Antarctic ice sheet ablated during MIS 5e, resulting in global sea levels that were ~6 m higher than present (Kopp et al., 2009; Muhs et al., 2011). That the LIG is only considered to be a partial analogue for future climate warming reflects the fact that the drivers of MIS 5e warmth (i.e. high insolation, some of the highest Middle/Late Pleistocene atmospheric greenhouse gas concentrations, coupled with enhanced ocean circulation) are not analogous to the drivers operating at present (i.e. low insolation and anthropogenically enhanced greenhouse gas concentrations). The palaeoclimatic dataset available for MIS 5e has been derived primarily from marine sea surface temperature (SST) records and high-latitude ice-

cores (Turney and Jones, 2010). Terrestrial records from which palaeoclimatic data have been obtained are less common and, where they are preserved, rely heavily on quantified temperatures derived from fossil assemblages . This is especially true for Europe, where the majority of terrestrial LIG records have been found, and for Britain in particular (Zagwijn, 1996; Aalberberg and Litt, 1998; Kaspar et al., 2005; Kühl and Litt, 2003; 2007; Kühl et al., 2007; Rousseau et al., 2007; Coope, 2010).

The British LIG record is particularly significant, since it has been suggested that this interval was at least 5^{o}C warmer than the 1961-1990 average (Turney and Jones, 2010). This is based on the abundance of fossils of themophilous flora and fauna that are now absent from Britain but common in southern Europe (Candy et al., 2010). In order to understand the magnitude of the warmth that characterised Britain during the LIG, the generation of precise palaeotemperature reconstructions is essential but also problematic. Such issues stem from the fact that techniques which use species assemblages to estimate warmest and coldest month temperatures frequently generate either 1) large ranges within which the true value may lie (Horne, 2007; Coope, 2010), or 2) temperature estimates with large associated uncertainties (i.e. modern analogue assemblage reconstructions of pollen (Kaspar et al., 2005; Kühl and Litt, 2007). The large ranges/uncertainties make it difficult to be confident about the absolute magnitude of LIG temperatures. Furthermore, temperature reconstructions based on individual indicator species frequently produce estimates of minimum summer or winter temperatures (see Candy et al., 2010) but say very little about the maximum temperatures.

LIG temperature estimates for Britain have been based on the analysis of a wide range of fossil groups (pollen, plant macrofossils, beetles, ostracods, reptiles and amphibians), however, no study has attempted to integrate the temperature data that can be derived from all of these lines of evidence. Whilst such an approach has to make assumptions about the direct comparability of temperatures derived from different fossils groups which use different

techniques for temperature reconstructions it does increase the number of thermophiles that can be incorporated into any reconstruction. This approach, therefore, has the potential to reduce the range/uncertainties of LIG palaeotemperatures and, therefore, provide more precise estimates of the thermal regime of Britain during this interval.

The focus of this paper is to review the record of thermophilous fauna and flora in the British record of the LIG. This review is based on the fossil groups that have been most routinely used by researchers to discuss the thermal regime of the LIG, primarily plant macrofossils, beetles, ostracods and herpetiles but also pollen based temperature quantifications. The overall aim of the paper is to generate high precision temperature quantifications for eight British LIG sites, allowing the thermal regime of Britain during this period of apparent global warmth to be discussed in greater detail. The paper describes the criteria for the selection of LIG sites and the proxies that are discussed and then presents coldest and warmest month temperature reconstructions for eight LIG sites. The paper concludes by discussing the significance of these temperature reconstructions in the context of; 1) present day temperature conditions, 2) estimates of the temperature regime of the Holocene thermal maximum and 3) modelling studies of British climates under future global warming. In particular the conclusion focusses on the similarities and differences between British LIG climates and future climate predictions and the issues of using MIS 5e as an analogue for future warming scenarios.

The Last Interglacial in Britain

The stratigraphy of the Last Interglacial in Britain

The LIG is represented in the British stratigraphic succession by deposits attributed to the Ipswichian interglacial (Mitchell et al., 1973). The recent recognition that pollen

biostratigraphy alone is unable to separate LIG sequences from those of earlier British interglacials such as MIS 7 (Sutcliffe, 1975; Green et al., 1984; Schreve, 2001a) has meant that British LIG deposits have been most reliably identified on the basis of mammalian biostratigraphy and amino acid racemisation (AAR) analysis (Sutcliffe, 1975; Currant and Jacobi, 2001; Schreve, 2001a, b; Penkman et al., 2011, 2013). LIG mammalian assemblages, included within the Joint Mitnor Mammal Assemblage Zone (MAZ), include *Hippopotamus amphibius* (Sutcliffe, 1959; 1975; Currant and Jacobi, 2001; Stuart, 1986; Schreve, 2001a, b), together with *Palaeoloxodon antiquus* (straight tusked elephant), *Stephanorhinus hemitoechus* (narrow-nosed rhinoceros), *Panthera leo* (lion), *Crocuta crocuta* (spotted hyaena), *Cervus elephas* (red deer), *Dama dama* (fallow deer) and *Megaloceros giganteus* (extinct giant deer). Absolute dating of the Joint Mitnor MAZ has been obtained through U/Th analysis of flowstone encasing hippopotamus fossils at Victoria Cave, Yorkshire, which yielded dates within MIS 5e (Gascoyne et al., 1981). Further dating support from AAR analysis of *Bithynia* opercula also places assemblages attributed to the Joint Mitnor MAZ within the LIG (Penkman et al., 2011, 2013). For the purposes of this study, Ipswichian/LIG sites are identified on the basis of the presence of vertebrate fossils attributable to the Joint Mintnor MAZ and/or AAR determinations.

It is important to note that the Ipswichian stage *sensu stricto* was defined on the basis of pollen biozone stratigraphy (West, 1957, 1980; Mitchell et al., 1973), an approach based on the premise that each interglacial had a unique vegetation history. Although palynology was fundamental to the initial subdivision of the Pleistocene successions of Britain and continental Europe, it has since been established that pollen records from different interglacials are often difficult to separate, resulting in deposits from different interglacial episodes being conflated into the same pollen-defined temperate stage (e.g. Sutcliffe, 1975; Thomas, 2001; Schreve, 2001a; Penkman et al., 2013). Several sequences that were

previously correlated with the Ipswichian interglacial on the basis of pollen evidence alone have more recently been reassigned, on the basis of faunal biostratigraphy and geochronology, to other interglacial stages including MIS 9 and 7 (Keen, 2001; Schreve, 2001; Candy et al., 2010). Consequently, although a large number of British sequences have historically been correlated with the Ipswichian (cf. Jones and Keen, 1993), this study includes only sites from which multiple lines of dating evidence have been obtained. Sites attributed to the LIG on the basis of pollen analysis alone, such as Wing, Mundesley and Wortwell (Phillips, 1976; Hall, 1980; 1986; Sparks and West, 1968) are considered to be of uncertain age and are therefore excluded from this dataset.

British Last Interglacial sequences

The interglacial episodes that are best represented within the British Quaternary record are the Ipswichian (MIS 5e) and the Hoxnian (MIS 11c). Despite its greater age, the Hoxnian is better understood than the Ipswichian, since it is represented by a number of long lacustrine sequences spanning the entirety (or a large part) of that interglacial (Candy et al., 2010, 2014). This can be attributed to the effects of the significant lowland glaciation that preceded the Hoxnian, during the Anglian Stage (MIS 12), which was the most extensive glaciation known to have affected central and eastern England (Bowen et al., 1986). The formation of numerous deep erosional basins and kettle holes on the post-glacial landscape (e.g. West, 1956; Turner, 1970; Candy et al., 2014) provided accommodation space within which sediments accumulated during the late Anglian, Hoxnian and, in some cases, the post-Hoxnian cold interval (Candy et al., 2014; Tye et al., 2016). Post-Hoxnian ice sheets were more limited in extent and did not advance over these sites, meaning that these lacustrine sequences are well-preserved within the British record (Pawley et al., 2008).

Because the Midlands and south of England were not affected by widespread lowland glaciation during MIS 6 (White et al., 2010, 2016), significantly less accommodation space was available in which Ipswichian interglacial deposits could accumulate. The sedimentary record of the LIG in Britain therefore mostly consists of fluvial deposits, such as abandoned channel fills and overbank sequences (Gibbard and Lewin, 2002). Although these represent ideal environments for the accumulation of fossil-rich sediments, and are therefore rich in palaeoenvironmental indicators, the sequences are invariably short, representing only part of the interglacial (Candy et al., 2010). Consequently, there are no sites at which a complete record of the Ipswichian interglacial is preserved; furthermore, most records represent only the early and middle parts of the interglacial, represented by pre-temperate (IpI) and early-temperate (IpII) pollen zones (Jones and Keen, 1993; Coope, 2001, 2010). The majority of Ipswichian sites record the early-temperate IpII phase of the interglacial, an interval that is widely considered to include the LIG thermal maximum (Zagwijn, 1996; Kaspar et al., 2005). IpII is characterised by *Corylus*-*Quercus*-*Pinus*, with *Acer* being a notable part of the pollen spectrum (West, 1957, 1980; Phillips, 1974, 1976).

Although pollen biostratigraphy is problematic as a means of distinguishing interglacial deposits of different ages, comparison of the vegetation succession remains a useful method for determining the relative positions of sequences of known age within a given interglacial (Turner and West, 1968). Palaeoclimatic studies of the Eemian, the continental correlative of the Ipswichian, have identified Eemian pollen zone IVa as the thermal maximum of this interglacial (Zagwijn, 1996; Kaspar et al., 2005). This zone is characterised by a distinct C*orylus* phase, which appears to be represented in Britain by Ipswichian zone IpIIb (West, 1957; Phillips, 1974, 1976). Varved lacustrine records spanning Eemian IVa suggest that this interval lasted for ~1150 years (Müller, 1974). The occurrence of the thermal maximum within the early temperate phase is supported by the fact that deposits with an IpII pollen

signature frequently contain a diverse range of exotic thermophilous taxa in their fossil assemblages (West, 1957; Franks, 1960; Zagwijn, 1996).

Palaeoecological evidence for last interglacial palaeotemperatures in Britain

Candy et al. (2010) divide the palaeoecological evidence for "enhanced warmth" that routinely occurs in the British interglacial sediments into two main categories. The first includes individual animal and plant species with specific temperature requirements for successful reproduction. These include reptile and amphibian species for which temperature exerts a control over egg incubation and hatching success, and plant species that require certain levels of warmth for successful germination/flowering/fruiting (Stuart, 1979; Meusel et al., 1978; Zagwijn, 1996; Aalberberg and Litt, 1988). The use of such indicators has two limitations. Firstly, the reproductive success or survival of these species is frequently controlled by the temperature regime of a single season, i.e. summer temperatures dictate the breeding success of many herptile species (Stuart, 1979), whilst winter temperatures control the survival of frost intolerant plant species (Iversen, 1944). Consequently, they can only be used to reconstruct parts of the thermal regime. Secondly, many other environmental parameters besides temperature dictate the successful establishment of a species within a region. Consequently, a high degree of caution must be exercised when using the presence of a single indicator species as a palaeoclimatic proxy (see Huntley, 2012).

For the purposes of this study previously published temperature requirements are accepted (Candy et al., 2010 and SI 1), albeit cautiously in some cases, such as *Trapa natans* (water chestnut). It has been noted that *T. natans* requires high summer temperatures of 20^{o}C or greater for successful fruiting (Meusel et al., 1978), suggesting that its presence within the fossil records implies equally warm summers. However, other studies have suggested somewhat lower temperature thresholds for germination and flowering (e.g. Galanti et al.,

1990; Karg, 2006). Since the ability to produce viable seeds will ultimately control the success of *Trapa*, it can be assumed that the higher value of ≥20°C is a requirement for its survival. It is worth noting that during the Holocene, and at the present day, established populations of this species have occurred outside the 20°C summer isotherm (Flenley et al., 1975; Korhola and Tikkanen, 1997; Schofield and Bunting, 2005). The recent distribution of this species in Europe has further been influenced by human cultivation since Neolithic times, and it is possible that anthropogenic impacts have become more significant that absolute temperature controls (Karg, 2006). Caution is therefore required when ascribing high summer palaeotemperatures to sites where *T. natans* is the only thermophilous species in the fossil assemblage. It is only at locations where such estimates are consistent with independent lines of evidence that such high estimates can be considered reliable.

The second category of evidence for 'enhanced warmth' includes data derived from assemblages of species. These use the known tolerances of the extant species in a given assemblage to calculate the possible temperature range within which all of these species could have co-existed (Atkinson et al., 1987; Sinka and Atkinson, 1999; Horne, 2007). In Britain this approach has been most widely applied to assemblages of beetle fossils from the Lateglacial and numerous Pleistocene interglacial stages through the pioneering work of G.R. Coope and the Mutual Climate Range (MCR) technique (Atkinson et al., 1987). A similar approach has been applied to fossil ostracod assemblages using the Mutual Ostracod Temperature Range (MOTR) method (Horne, 2007; Horne et al., 2012). The advantage of these approaches over the use of a single indicator species is that they incorporate the environmental tolerances of several species to produce a more reliable temperature estimate. However, the precision of these estimates is dependent on the number of species present within an assemblage for which well-constrained ecological data are available. It is also important to note that both the MCR and MOTR methods generate temperature ranges for

Tmax and Tmin, with the absolute value lying somewhere within that range but with no value being the "likeliest" outcome; it is therefore unsafe to assume that the median point of a given range is the most probable Tmin/Tmax value. The climatic tolerances of important indicator species found within Ipswichian interglacial deposits are summarized in SI1. Whilst in other regions and in Britain for different time intervals (i.e. the Holocene and Lateglacial) palaeoclimatic reconstructions based on transfer function techniques, i.e. chironomids, and modern analogue assemblages, i.e. pollen, are widely used (Birks et al., 2010) these approaches are not discussed here as they have had minimal application to the pre-Holocene interglacial deposits of the British Quaternary (see discussion and Kaspar et al., 2005). Such approaches clearly have the potential to add further detail to the reconstruction of British interglacial climates in the future.

Methodology

This review only includes sites (Figure 1 and SI 2) that meet the following three criteria: firstly, the site must be securely dated to the LIG on the basis of mammalian biostratigraphy, aminostratigraphy and absolute dating (Keen et al., 1999; Currant and Jacobi, 2001; Penkman et al., 2011, 2013). Secondly, the sequence must have yielded pollen evidence indicating that the sediments accumulated during the early temperate phase of the interglacial (IpII), so that palaeotemperature evidence from any associated fossil assemblages relates to conditions that existed at, or close to, the thermal maximum (West, 1957, 1980; Phillips, 1974, 1976). Finally, the record must include fossils from which quantitative temperature estimates can be calculated, ideally from multiple, independent proxies.

Six British localities meet these criteria; Trafalgar Square, London (Franks, 1960; Preece, 1999), Bobbitshole, Ipswich, Suffolk (West, 1957; Coope, 1974; Stuart, 1979), Swanton

Morley, Norfolk (Phillips, 1976; Coxon et al., 1980), Woolpack Farm, Fenstanton, Cambridgeshire (Gao et al., 2000), Deeping St James, Lincolnshire (Keen et al., 1999) and Tattershall Castle, Lincolnshire (Girling, 1974; Holyoak and Preece, 1985). In addition, the sites at Shropham and Itteringham (both in Norfolk) are considered, for which only unpublished data are available (Beesley, 1988; Walkling, 1996); although both sites have yielded beetle faunas suitable for palaeotemperature reconstructions, they lack pollen data from the associated sediments. Attribution of the site at Austerfield (Coope, 2001, 2010) is controversial and it is therefore excluded from this study. .

Palaeoecological data was compiled from published species lists and from unpublished sources available via online databases (e.g. http://www.bugscep.com). For single indicator species, published temperature requirements have been applied (SI1). Temperature thresholds based on plant species were only applied when macrofossils identified to species level were recorded; for example, species such as *Acer monspessulanum* (Montpellier maple), *Ilex aquifolium* (European holly) and *Hedera helix* (European ivy) are known to be sensitive to both winter and summer temperatures (Iversen, 1944; Zagwijn, 1996; Candy et al., 2010), but the presence of pollen of *Acer* sp., *Ilex* sp. and *Hedera* sp., which occur in most IpII pollen successions (Phillips, 1974; West, 1980; Gao et al., 2000) was not considered sufficient. At present, only *I. aquifolium* and *H. helix* occur in northern Europe, raising the possibility that it can be assumed that these species are represented in Pleistocene pollen successions; however, it remains unclear whether this biogeographical distribution was the case during pre-Holocene interglacials. Consequently, we restrict the application of these tolerances to sites where macrofossils of these species occur.

For fossil beetle and ostracod assemblages, Tmax and Tmin ranges were calculated afresh for this study using the MCR and MOTR methods respectively (see Atkinson et al., 1987; Horne, 2007; Coope, 2010; Horne et al., 2012) using available species lists (see SI 3). In some cases

this has resulted in estimates that differ from those previously published for the same assemblage; this is a crucial point which will be addressed below in the discussion. It is also important to note that not all of the species recorded in LIG deposits have MCR temperature envelopes, meaning that not all potentially usable species can be incorporated into temperature calculations. It is important to note that whilst many of the fossil groups used in this study are aquatic and, therefore, record water temperatures, for the purposes of this study it is assumed that these equate to air temperature. This is proposed because in mid-latitude, temperate lowland river systems water temperatures rapidly equilibrate with air temperatures and are, therefore, equivalent (see Waghorne et al., 2012). This is not necessarily true of lake waters (see Candy et al., 2015) but as all sequences discussed here at fluvial in origin this is not considered significant. Site data and palaeoclimate reconstructions are summarised in SI2 and Figure 2.

Palaeotemperature estimates from British LIG sites

The sequence at Trafalgar Square has yielded the most diverse record of thermophilous flora and fauna of any British LIG site (Franks, 1960; Preece, 1999; Candy et al., 2010). Beetle assemblages provide MCR Tmax values of +17 to +21^{o}C and Tmin values of -6 to +3^{o}C, whilst the ostracod assemblage provided MOTR Tmax values of +12 to +23^{o}C and Tmin values of -1 to +5^{o}C. The plant macrofossil assemblages include *Najas minor* and *Trapa natans*, which require summer temperatures of ≥18^{o}C and ≥20^{o}C respectively, as well as *Hedera helix*, which is intolerant of winter temperatures below 1.5 to 2^{o}C. All of these fossils were recovered from channel fill deposits from which a pollen assemblage characteristic of IpII was also obtained; the pollen record showed no evidence for major vegetational change during the accumulation of the sequence (Franks, 1960). The fossils are

therefore considered to be contemporaneous with each other, allowing the temperature tolerances of all of the species that occur at Trafalgar Square to be combined to yield Tmax and Tmin estimates of +20 to +21^{o}C and +1.5 to +3^{o}C respectively (Figure 2).

Data from Deeping St James, Tattershall Castle and Woolpack Farm yielded similar palaeotemperature results and are therefore considered together. All three sequences represent interglacial river channels in the Welland, Witham and Great Ouse systems, respectively. The pollen assemblages from each site are dominated by *Corylus-Quercus-Pinus*, typical of pollen substage IpII, refined to IpIIb in the case of Deeping St James and Tattershall Castle. Multiple beetle assemblages were recovered from all three sequences; MCR Tmax and Tmin estimates are shown in Figure 3. The beetles yielded Tmax and Tmin estimates with large ranges (Figure 3). The Tmin ranges of most samples are in the order of 10-20 ^{o}C. At all three sites, however, at least one sample provided Tmax/Tmin estimates with smaller ranges, typically samples that contain the highest number of species. These samples (MH at Tattershall Castle, WP0502 at Woolpack Farm and Bulk and S15-30 at Deeping St James) yielded identical Tmax and Tmin estimates of +17 to +18^{o}C and -4 to +4^{o}C. The Tmax/Tmin estimates with the smallest ranges fall within (and are therefore entirely consistent with) the temperature ranges based on other beetle samples from the same sites (Figure 3). Since all three sites are characterised by pollen records representing deciduous temperate woodland, it is likely that Tmin could not be lower than -2.5 ^{o}C (see SI1). Both Woolpack Farm and Tattershall Castle yielded macrofossils of *Acer monspessulanum*, and *Najas minor* occurs at Deeping St James (Holyoak and Preece, 1985; Keen et al., 1999; Gao et al., 2000). The temperature requirements of these species (Figure 2) are consistent with the Tmax estimates of +17 to +18^{o}C. The ostracod assemblage from Tattershall Castle provided MOTR Tmax and Tmin values of +16 to +22^{o}C and -1 to +4^{o}C respectively, consistent with the beetle-based estimates, albeit with much wider ranges.

At Bobbitshole (West, 1957; Coope, 1974), beetle assemblages provide MCR Tmax and Tmin estimates of +17 to +27^{o}C and -7 to +9^{o}C respectively. High summer temperatures are supported by the presence of *Emys orbicularis* (European pond tortoise) and plants such as *Najas minor*, *Acer monspessulanum* and *Salvinia natans* (West, 1957). The large range of both the Tmax/Tmin estimates from Bobbitshole reflect the limited number of species (n = 6) that can be incorporated into MCR calculations. At Swanton Morley, Ipswichian channel deposits of the river Wensum have yielded fossil remains of *E. orbicularis* and *T. natans* (Phillips, 1976; Coxon et al., 1980), suggesting summer temperatures of ≥18 ^{o}C and ≥ 20^{o}C respectively (Stuart, 1979; Coxon et al., 1980). Swanton Morley and Trafalgar Square are the only localities included in this study to have yielded remains of *T. natans* (although see Sparks and West, 1968), the indicator species with the highest threshold for minimum summer temperatures (SI1 and 2). The *T. natans* fossils from Swanton Morley were associated with pollen zone IpIIb, whereas the *E. orbicularis* remains occurred in the earlier IpIIa pollen zone.

As mentioned above, beetle assemblages from Itteringham and Shropham (both in Norfolk) can be used to calculate MCR temperature estimates, but these were not associated with any pollen evidence. Consequently, the position of the derived palaeotemperature estimates within the Ipswichian interglacial cannot be established with certainty, and their correlation with the other sequences described here is unclear. However, both sites yield very similar Tmax and Tmin estimates; Shropham – Tmax +17 to +18^{o}C and Tmin -4 to 0^{o}C; Itteringham – Tmax +17 to +19^{o}C and Tmin -5 to +1^{o}C. At both sites, Tmax estimates are supported by the presence of *E. orbicularis* (Hallock et al., 1990; Holman and Claydon, 1990). Furthermore, these estimates are comparable to the Tmax and Tmin estimates with the smallest ranges from Deeping St James, Tattershall Castle and Woolpack Farm.

Discussion

Internal consistency of Ipswichian palaeotemperature estimates

The palaeotemperature estimates presented here follow an approach that is widely applied in Quaternary studies and which makes two key assumptions: firstly, it assumes that the temperature controls on a given species are well understood and that temperature is the primary factor limiting the distribution of that species in the past; secondly, it adheres to the uniformitarian principle that the modern ecological tolerances observed for a given species have not evolved or changed over time (see Candy et al., 2010; Huntley, 2012). These assumptions are fundamental to many areas of palaeoeocology, but in the context of this study they can be partially tested through comparison of palaeotemperature estimates derived from multiple independent proxies. In this respect, the quantified values presented above are entirely consistent; at no site is there a situation where different fossil proxies have provided incompatible palaeotemperature estimates. This is particularly true for Trafalgar Square, which has yielded the richest assemblage of thermophilous indicator species, providing multiple lines of evidence for Tmax and Tmin estimates.

At sites where beetle Tmax ranges are small, the inter-site distribution of thermophilous flora appears to match these estimates very precisely. For example, at Deeping St James, Tattershall Castle and Woolpack Farm the Tmax range of +17 to +18 ^{o}C is incompatible with the presence of *Trapa natans*, which requires summer temperatures of ≥20 ^{o}C in order to fruit successfully. Accordingly, *T. natans* is absent at these sites and the thermophilous plant species present have slightly lower summer temperature requirements compatible with those of the beetle faunas. The only site that has provided beetle Tmax estimates warm enough for the successful growth of *T. natans* is Trafalgar Square, and this is indeed the only British LIG site included in this study where this species is present. The close agreement of

palaeotemperature estimates derived from multiple independent proxies therefore suggests that the combined estimates presented here are generating reliable Tmax and Tmin estimates and that these are a valid basis for a discussion of British LIG climates.

The palaeotemperature regime of the Ipswichian/LIG in Britain

Palaeoenvironmental and palaeoclimate modelling studies commonly compare reconstructed palaeotemperatures with modern day conditions. All of the localities at which LIG sequences are preserved are characterised by modern day coldest month temperatures (January) of +3 to +4^{o}C and warmest month temperatures (July) of +16 to +17^{o}C, with the exception of the London basin, where temperatures slightly exceed these values due to a significant urban heat island effect. The LIG data are compared with UK meteorological mean monthly temperature data (1961-1990) in Figure 4, allowing two key observations to be made. Firstly, it is clear that all LIG sites provide Tmax estimates in excess of modern day Tmax values, although the magnitude of this enhanced summer warmth varies. Secondly, all Tmin estimates have large ranges making it difficult to precisely quantify the magnitude of winter temperatures. However, at no site is the upper limit of the Tmin greater than modern Tmin values. Consequently, winter temperatures during the LIG must have been cooler than or the same as modern Tmin values, but not warmer. Given that LIG sites have yielded Tmax estimates greater than modern day values but Tmin estimates than are the same as or cooler than modern day values, the dataset implies that the LIG in Britain was a period of increased seasonality relative to the present. This is best seen in the difference between Tmax and Tmin at Trafalgar Square; modern day seasonality (Tmax – Tmin) in southern Britain is 12 to 14^{o}C, whereas at Trafalgar Square seasonality is 17 to 20^{o}C. Although the degree of seasonality is lower for other LIG sites, it is routinely greater than the present day.

With respect to Tmax, the majority of sites (Deeping St James, Woolpack Farm, Tattershall Castle, Shropham and Itteringham) indicate that summer warmth is ~0-2^{o}C greater than present. It should be noted that at both Woolpack Farm and Tattershall Castle, despite the presence of numerous themophilous taxa, the lower limit of the Tmax range is 17^{o}C, the same as the upper limit of the modern Tmax range. At both of these sites it is therefore possible that Tmax values were the same as the present. Trafalgar Square is the site that records the most reliable evidence for enhanced summer warmth, the low range of Tmax estimate from this site (20-21^{o}C) suggests that, during the deposition of the sediments at this site, mean warmest month temperatures were 3-5^{o}C warmer than the present. At Bobbitshole the large range of the Tmax reconstruction (+18 to +27^{o}C) makes it impossible to establish whether this site is comparable to Trafalgar Square (with Tmax 3-5^{o}C warmer than the present) or more like the majority of LIG sites which record Tmax values of c~18^{o}C.

At Swanton Morley, the occurrence of *Trapa natans* in association with an IpIIb pollen signature might imply that summer temperatures were ≥20^{o}C; however, since *T. natans* is the only thermophile present in this deposit, this estimate is not supported by other independent lines of evidence. The climatic significance of *T. natans* is important to understanding the thermal maximum of the LIG since 1) it is the only thermophilous species that is used to suggest such high (≥20^{o}C) Tmax values, and 2) its climatic significance has been questioned (see above; Candy et al., 2015). Excluding *T. natans*, Tmax estimates for Trafalgar Square would be +18 to +21^{o}C, the lower end of this range being consistent with the Tmax estimates for most other LIG sites presented here. Researchers have debated the relative roles of human agency, water quality and direct insolation versus air temperature in controlling the distribution of *T. natans* (see Candy et al., 2015 for detailed discussion). The Tmax reconstruction presented here therefore assumes that the summer temperature requirement of

≥20ºC for *T. natans* is reliable and implies strong summer warmth during the deposition of the Trafalgar Square sequence.

If the reliability of the Tmax and Tmin values presented here are accepted (with appropriate caution), then it is clear that the time period represented by the Trafalgar Square sequence cannot be synchronous with those recorded at other Ipswichian sites. The thermal maximum of the Ipswichian (IpII) must be recorded at Trafalgar Square, although the levels of warmth recorded at this site were clearly not sustained for the entirety of the IpII, since summer temperatures at all other sites of this age are slightly cooler. It is therefore likely that the thermal maximum of the Ipswichian, represented in Britain at Trafalgar Square, was short-lived. Although regional correlations of terrestrial records are extremely difficult to establish, it is worth considering that the continental equivalent of IpII, Eemian zone IVa, lasted for ~1200 years (Müller, 1974). If we assume that this also applied to Britain then the summer temperature regime 3-5ºC warmer than the present day may have lasted for <1200 years during the LIG.

Comparison with previous estimates of Ipswichian/Eemian temperatures

Climatic reconstructions for the LIG in Europe and Britain have been proposed elsewhere, although recent work (e.g. Rousseau et al., 2007; Brewer et al., 2008) was focused on latitudes south of the British Isles and is therefore not directly relevant here. Climatic reconstructions for the Eemian in Europe have included pollen-based temperature reconstructions from sites across Europe, including British localities (Kaspar et al., 2005) and plant macrofossil based reconstructions for western Europe (Zagwijn, 1996; Aalbersberg and Litt, 1998). Similarly, Coope (2000; 2001; 2004; 2010) has provided beetle temperature estimates for Britain. The Kaspar et al. (2005) and Zagwijn (1996) studies included only up to four British sites one of which (Selsey) is now considered to be of MIS 7 age.

Furthermore, the site of Wing (Hall, 1980), included in the Kaspar et al. (2005) dataset, cannot be confidently correlated with MIS 5e, its attribution being based entirely on pollen stratigraphy; indeed, the relationship between the Wing interglacial deposits and the Wragby Till of eastern England has been used to suggest a tentative MIS 7 age for this sequence (White et al., 2016). This is important to note, since palaeoclimate reconstructions from these sites have been incorporated into global databases for the LIG (Turney and Jones, 2010). The only British sites included by Kaspar et al. (2005) that are of definitive LIG age are Stone (Hampshire) and Bobbitshole; pollen modelling studies from both sites suggests Tmax values between 2.5 and 3^{o}C warmer than present and Tmin values ~2^{o}C cooler than present. These estimates match the patterns of enhanced LIG seasonality described above and are consistent with the Tmax values reconstructed from the Trafalgar Square fossil assemblages. Zagwijn (1996) generated Tmax and Tmin curves for the Eemian in the Netherlands, which indicate that Eemian pollen zone IVa-IVb experienced the highest summer temperatures of the entire interglacial, ~2^{o}C warmer than present. This interval was, again, a period of enhanced seasonality, with Tmin values being the same as or up to 1^{o}C cooler than the present day; the reconstructions presented here are therefore comparable with those suggested by Zagwijn (1996)

The palaeotemperature reconstructions presented in this study are heavily reliant on beetle assemblages analysed by Prof G.R. Coope over many decades (Coope, 1974, 2001, 2010, Taylor and Coope, 1985; Keen et al., 1999; Gao et al., 2000). This work is fundamental to our understanding of British interglacials and has provided the most routinely used palaeotemperature estimates for temperate episodes (Coope, 2001; 2006; 2010). All of the beetle assemblages reported here were derived from work carried out by Coope at individual sites and summarised in a number of influential reviews. For the LIG, these studies frequently quote Tmax values of ~21^{o}C and Tmin values the are the same as, or a degree or so cooler

than, the present day (Coope, 1974, 2001, 2010; Keen et al., 1999; Gao et al., 2000). It is important to note that, with respect to Ipswichian beetle assemblages, Coope rarely used the MCR method to calculate Tmax and Tmin ranges, preferring temperature estimates based on the modern distribution of thermophilous species and a semi-qualitative assessment of the most likely temperature values (see Coope, 1974, 2010; Keen et al., 1999; Gao et al., 2000). Some studies (e.g. Keen et al., 1999) have argued that this approach is more valid because the northerly range of many of the thermophilous species was poorly constrained, causing Tmax estimates based on strict MCR estimates to be artificially low. Where LIG MCR estimates are presented, i.e. for Shropham (Coope, 2000) the results overlap with those presented here but with much larger Tmax and Tmin ranges (+18 to +24^{o}C and -6 to +6^{o}C). The difference reflects the fact that this study uses the complete species list for the Ipswichian deposits at Shropham, whereas Coope (2000) selected a species assemblage that was assumed to represent the early (IpII) interglacial. No pollen record exists for this part of the Shropham sequence and so this study makes no attempt to separate assemblages of species from the overall Shropham Ipswichian list.

At Trafalgar Square, the MCR based Tmax and Tmin estimates, when combined with the evidence derived from thermophilous plant macrofossils, match exactly those proposed by Coope (2010). However, this site is unique in having such high Tmax estimates, with all other British LIG sequences yielding MCR Tmax estimates several degrees cooler than the +21^{o}C Tmax estimate proposed by Coope. It should be noted that for several sites for which suggested Tmax values of +21^{o}C have been published, closer inspection of the data reveals that they either have large Tmax ranges (e.g. Bobbitshole) or have smaller ranges but are colder than the quoted value of +21^{o}C (i.e. Deeping St James, Tattershall Castle, Woolpack Farm).

Tmax estimates with large ranges are often based on datasets with low species diversity. At Tattershall Castle, for example, all the samples that yield Tmax estimates with a range of 8°C or greater are based on ≤7 species. The only sample from Tattershall Castle (MH) that has a Tmax estimate with a range of only 1°C is based on the largest species assemblage (n = 19). The geographical/climatic extent of the individual species within an assemblage is, however, just as significant in controlling Tmax and Tmin ranges. A large assemblage made up of eurythermic species will generate MCR Tmax and Tmin estimates with larger ranges than those calculated from a small assemblage made up of stenothermic species. For example, at Deeping St James sample S15-30 contains 18 species that can be used in MCR calculations, generating a Tmax of +17 to +18°C, whilst samples S30-45 and S45-top, from the same site, contain >20 species but both yield Tmax values of +17 to +24°C. The difference between these samples is the presence, within the former, of the beetle species *Platystethus aranarius*, with a modern distribution from the arctic tundra to the cooler parts of central Europe and a temperature envelope of +9 to +18°C. It is only the presence of this species which generates a Tmax with a range of 1°C. *Platystethus aranarius* also occurs at Tattershall Castle (sample MH) but in none of the other samples from this site; again, it is the presence of this cold tolerant species that reduces the calculated Tmax range (+17 to +18°C). At Woolpack Farm the Tmax and Tmin estimates with the lowest ranges (sample WP0502) include another species, *Platystethus nodifrons*, that is also tolerant of cool conditions and whose modern range yields a Tmax of +9 to +18°C. This species is absent from all other beetle samples at Woolpack Farm which generate Tmax estimates with much larger ranges. *Platystethus nodifrons* has also been recorded Shropham. Although Ipswichian beetle assemblages are rich in thermophilous species currently distributed in southern Europe (Coope, 1974, 2001, 2010), for the majority of IpII sites (Deeping St James, Tattershall Castle, Woolpack Farm, Itteringham and Shropham) it is the presence of these thermophiles in association with

occasional cold adapted species that 1) produces Tmax estimates with low ranges, and 2) results in Tmax estimates only ~1^{o}C higher than present. At Trafalgar Square the beetle species that can be used in MCR calculations, 43 in total, contain none of the northern/cold adapted species described above. However, even at this site it is the combination of the MCR reconstruction and the associated presence of exotic flora that reconstructs a Tmax for IpII at this site of +20 to +21^{o}C.

Ipswichian palaeotemperatures in the context of models of Holocene and future warming

Many of the thermophilous species that characterise the Ipswichian are absent from British deposits of the current interglacial (Godwin, 1975; West, 1997). Whilst it is true that *Najas minor*, *Salvinia natans*, *Acer monspessulanum* and the majority of the southern European beetle species discussed above do not appear to have been part of the Holocene flora and fauna of Britain, both *Emys orbicularis* and *Trapa natans* have been documented from deposits of the current interglacial. Significantly, however, each has been found only at a single site; East Wretham (Norfolk) in the case of *E. orbicularis* (Stuart, 1979) and the Skipsea meres (East Yorkshire) in the case of *T. natans* (Flenley et al., 1975; Schofield and Bunting, 2005). Furthermore, they are the only thermophilous species present at these sites that suggest that the mid-Holocene climate was warmer than the present day. The first point is significant, since the Holocene is well-studied in Britain, with an extensive number of sites dated to this interval, only two of which have yielded LIG-type thermophilous species. The scarcity of such species in the British Holocene therefore appears to be a real phenomenon. In contrast, there are far fewer sites dated to the LIG and yet three of these are known to contain *E. orbicularis* and two have yielded *T. natans*.

The second point is also important because, as has been outlined earlier, ascribing a temperature control to the presence of a single thermophilous species, when other

environmental factors, could also be the dominant control is problematic. In the case of the Ipswichian it is the co-occurrence of multiple thermophilous species and the consistency of the temperature estimates that they yield that adds weight to the palaeoclimatic reconstruction. Whilst the presence of *E. orbicularis* and *T. natans* at sites such as East Wretham and Skipsea could imply enhanced summer temperatures, the lack of supporting climatic evidence at these sites makes such interpretations difficult to justify.

It is important to consider, however, that at East Wretham and Skipsea these thermophiles occur in association with Fl II (Fl denotes the Flandrian interglacial, the British stratigraphic term for the current interglacial, with Fl II representing the early temperate phase of the Flandrian) or the Atlantic of the Blytt-Sernander system (Godwin, 1975; West, 1980; Jones and Keen, 1993). Fl II represents the interval between 8,000 and 6,000 yrs B.P. which is proposed to represent the Holocene thermal maximum in Britain (Figure 5; Hibbert et al., 1971; West, 1977; Davis et al., 2003; Mauri et al., 2015). In a number of pollen-based climate modelling studies (e.g. Davis et al., 2003) it has been argued that, during the Atlantic, summer temperatures were 1-2^{o}C warmer than those of the present whilst winter temperatures were ca 1^{o}C cooler (West, 1980; Davis et al., 2003; Mauri et al., 2015). Summer temperatures of such a magnitude would be sufficient to allow successful breeding within populations of *E. orbicularis*, whilst this warmth combined with favourable local conditions, i.e. nutrient availability, may also have allowed local populations of *T. natans* to develop (see Flenley et al., 1975; Schofield and Bunting, 2005; Karg, 2006 for discussion).

The Tmax and Tmin estimates for the Holocene thermal maximum in Britain are consistent with many of the temperature reconstructions for LIG sites presented here (Figure 5). This would imply that although the reconstructed temperature regime for some LIG sites (e.g. Tattershall Castle, Woolpack Farm, Deeping St James) was different to the present day, it may not have been incompatible with that of the Holocene thermal maximum. However, the

degree of summer warmth recorded at a site such as Trafalgar Square appears to have been in excess of that experienced in Britain at any point in the Holocene. The thermal peak of the Ipswichian can, therefore, be said to have been warmer than that of the current interglacial, although it is important to highlight that such a suggestion is strongly dependent on the fossil record of a single site.

The LIG is often cited as being a partial analogue for future global warming (Kopp et al., 2009) as it is clearly an interval of enhanced warmth (Masson-Delmotte et al., 2006; 2010; Lunt et al., 2013). The evidence for enhanced summer warmth at sites like Trafalgar Square, 3-5^{o}C warmer than the present day, support this. There is a good degree of consistency between such a reconstruction and predictions of future warmth. For example, the majority of climate modelling studies indicate that under medium emission scenarios, i.e. A1B of IPCC 2007 or RCP 4.5/6.5 of IPCC 2013, summer temperatures in Britain are likely to increase by 2-3^{o}C relative to the present day by 2100 (see also Raper et al., 2000 for a summary of early research). The major difference between the LIG thermal maximum and future warming scenarios in Britain is in the pattern of winter temperatures. Whilst most modelling scenarios indicate that by 2100 winter temperatures in Britain will increase by ca 3^{o}C relative to the present, all LIG Tmin reconstructions for Britain indicate that winter temperatures were the same as, or in all probability cooler than, modern day conditions. The pattern of warmth that Britain experienced during the LIG is not, therefore, analogous with future warming scenarios for this region.

In summary, the climate of the "peak" Ipswichian is characterised by warmer summers, cooler winters and enhanced seasonality, a pattern supported by the modelling studies of Kaspar et al. (2005) and Lunt et al. (2013) and temperature reconstructions of Zagwijn (1996). In contrast, all climate modelling predictions indicate that by 2100 Britain will be characterised by warmer summers, warmer winters and, therefore, unaltered or, in all

probability, *reduced* seasonality. That the thermal maximum of the Ipswichian is characterised by increased seasonality is consistent with the fact that peak interglacial conditions occured in association with a major peak in summer insolation, and therefore a major low in winter insolation. This configuration, even when the relatively high atmospheric concentrations of CO_2 and CH_4 are taken into consideration, has the potential to produce enhanced seasonality. This situation is not analogous to the current warming which occurs in association with moderate levels of both winter and summer insolation and atmospheric concentrations of CO_2 and CH_4 that are uniquely high for the past 800,000 yrs. In many regions of the world the LIG may provide a useful analogue for current/present warming and the response of Earth systems within a warmer world (Kopp et al., 2009; Lunt et al., 2013; Capron et al., 2014), however, the enhanced seasonality of the Ipswichian produces a climatic setting that is unlikely to be analogous to the climate of Britain in the 21st century and beyond.

Conclusions

A review of the thermophilous flora and fauna from LIG deposits in Britain allows the following conclusions to be drawn. There is good evidence to suggest that the climate of Britain during the LIG was warmer than that of the present day. At only one site (Trafalgar Square, London), however, is there convincing evidence that the degree of warmth that Britain experienced during the LIG was greater than that which occurred during the Holocene thermal maximum. Furthermore, evidence for enhanced warmth is entirely in Tmax reconstructions (3-5^{o}C warm than present) with Tmin estimates being the same as or cooler than the present. As a result LIG climates are characterised by greater seasonality than the present day. Although the LIG is considered a partial analogue for future climate warming, the reconstructed palaeotemperature regimes (typified by warmer summers, cooler winters and enhanced seasonality) are not consistent with those predicted for Britain in 2100 (warmer

summers, warmer winters, unchanged or reduced seasonality). The LIG may provide a useful for analogue for current/present warming and the response of the Earth system in a warmer world but in Britain, at least, the climate of the LIG appears to be non-analogous to that of future climate predictions.

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Supplementary Information

SI1 – Temperature requirements of the themorphilous indicator species used in this study.

SI2 – Stratigraphic, sedimentary and palaeoecological information of all the sites referred to in this study.

SI 3- The list of beetle and ostracod species used to calculate Tmax and Tmin for British MIS 5e sites using MCR or MOTR.

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Figure captions

Figure 1 – The location of the key LIG (Ipswichian) sites included in this study. MIS 7 and Holocene sites discussed in the text are also shown.

Figure 2 – Summary of Tmin and Tmax estimates from LIG (Ipswichian) sites discussed in this study. The red and blue zones represent the most probable range of Tmax and Tmin, respectively, once the climatic tolerances of all the thermophiles are taken into consideration. The vertical green line represents the lowermost winter temperature under which the development of deciduous woodland is likely to occur (Prentice et al., 1992). See SI1 for summary of the environmental tolerances of the different thermophiles, and SI2 for site details.

Figure 3 – Graphic depiction of the Tmax and Tmin of all the beetle sub-samples from Deeping St James, Woolpack Farm, Fenstanton and Tattershall Castle. The figure shows that most of the subsamples a have large ranges for both Tmax and Tmin but at each site at least one sample occurs that has sufficient species of a restricted enough range to produce more tightly constrained ranges. These yield identical Tmax and Tmin values for each of three sites

(Tmax = +17 to +18^{o}C; Tmin = -4 to +4^{o}C). At all three sites Tmin can be further constrained by the presence of deciduous woodland (=/>-2.5^{o}C) and the ostracod MOTR values at Tattershall Castle (-1 to +4^{o}C).

Figure 4 – Comparison of Tmax and Tmin from Ipswichian sites with modern day Tmax and Tmin from southern and eastern England. At all sites Tmax values support the idea that summers were warmer than the present day although the degree of difference varies between sites. The range of reconstructed Tmin values are much greater. In many cases the upper limit of the Tmin estimate may be consistent with present day values, however, most sites also offer the possibility of winter temperatures that are significantly cooler than the modern. All sites suggest a greater degree of seasonality.

Figure 5 – a) A comparison between Ipswichian Tmax and Tmin estimates and reconstructed summer and winter temperatures for the Holocene (Mauri et al., 2015). Holocene summer (white boxes) and winter (black boxes) temperatures are taken from projections by Mauri et al. (2015) after Davis et al. (2003). The figure uses temperature anomaly estimates for JJA and DJF for southeast England converted into absolute temperatures by adding the anomaly to temperature estimates. Note that this comparison is for diagrammatic purposes only because Ipswichian values are Tmax and Tmin (warmest and coldest months), whereas the Holocene values are summer and winter estimates. The main aim of the figure is to show that the Tmax temperatures reconstructed from the deposits at Trafalgar Square have no comparable analogue in the Holocene but that the Tmax estimates from most other IpII sites are consistent with the warmth that occurred during the Holocene thermal maximum (the Atlantic). Less can be said about Tmin because of the large ranges that exist for many estimates, however, it appears that the enhanced seasonality that is associated with high Tmax values in the Ipswichian is also seen in the Holocene. b) Data from a) plotted as climatic envelopes, again this shows that the Tmax of most IpII sites are warmer than the

present day but consistent with Fl II (the Holocene thermal maximum in Britain). This plot also shows that Tmax for Trafalgar Square is higher than any Holocene reconstruction, whilst the Tmin value is lower than the present day, highlighting the enhanced seasonality recorded at this site.

Figure 1


Victoria Cave
Skipsea
MIS 7 sites
MIS 5e sites
Holocene sites
N
NORTH SEA
Tattershall Castle
Mundesley*
Itteringham
Swanton Morley
Elsing
Deeping St James
Wing*
Shropham
East Wretham
Wortwell*
Woolpack Farm
Bobbitshole
Trafalgar Square
Stone
Selsey
ENGLISH CHANNEL

Figure 2

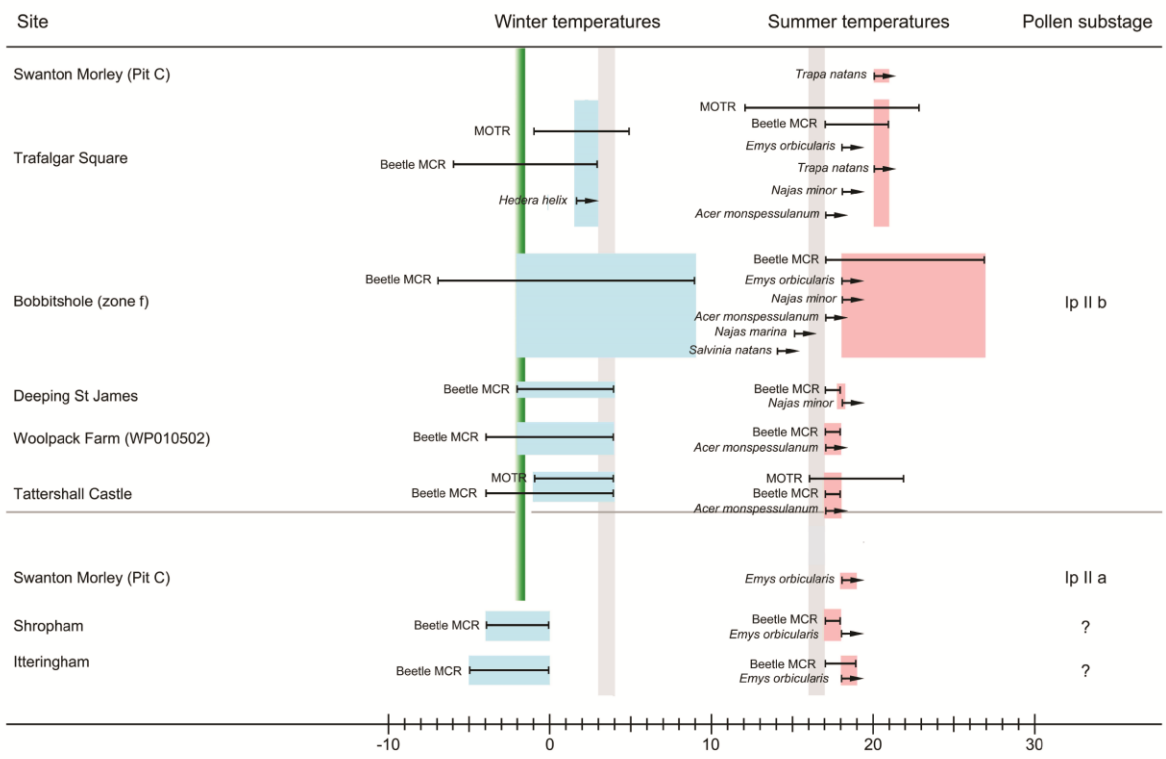

Site
Winter temperatures
Summer temperatures
Pollen substage
Swanton Morley (Pit C)
Trafalgar Square
Bobbitshole (zone f)
Deeping St James
Woolpack Farm (WP010502)
Tattershall Castle
Swanton Morley (Pit C)
Shropham
Itteringham
MOTR
Beetle MCR
Hedera helix
Trapa natans
Emys orbicularis
Najas minor
Acer monspessulanum
Najas marina
Salvinia natans
lp II b
lp II a
?
-10
0
10
20
30

Figure 3

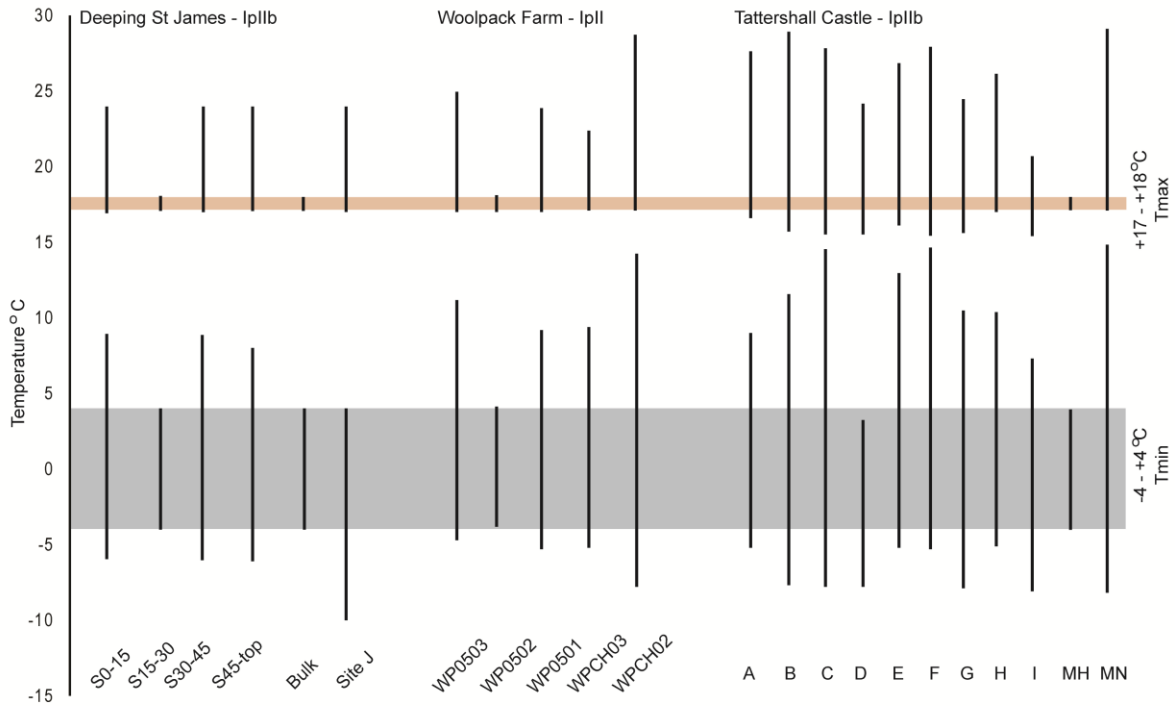

Deeping St James - IpIIb
Woolpack Farm - IpII
Tattershall Castle - IpIIb
Temperature ° C
30
25
20
15
10
5
0
-5
-10
-15
+17 - +18°C
Tmax
-4 - +4°C
Tmin
S0-15
S15-30
S30-45
S45-top
Bulk
Site J
WP0503
WP0502
WP0501
WPCH03
WPCH02
A
B
C
D
E
F
G
H
I
MH
MN

Figure 4

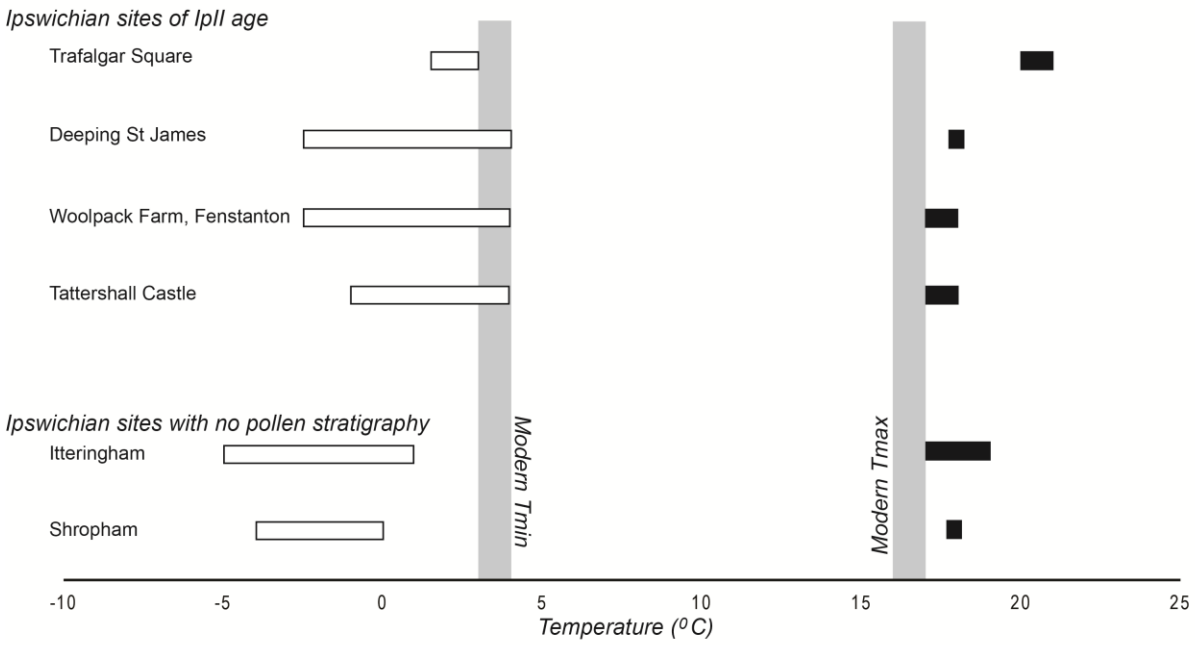
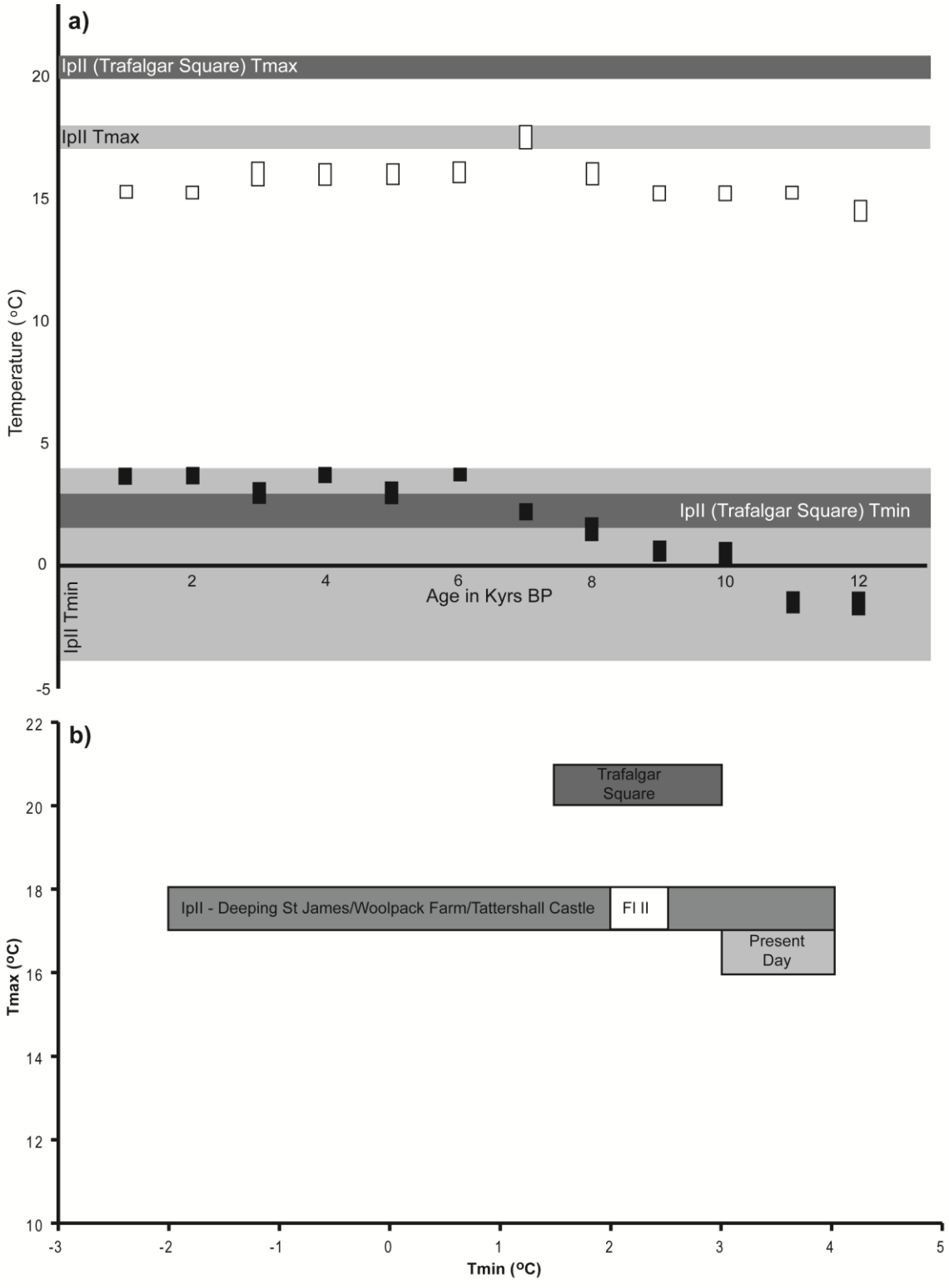

Ipswichian sites of IpII age
Trafalgar Square
Deeping St James
Woolpack Farm, Fenstanton
Tattershall Castle
Ipswichian sites with no pollen stratigraphy
Itteringham
Shropham
Modern Tmin
Modern Tmax
-10
-5
0
5
10
15
20
25
Temperature (⁰C)

Figure 5


a)
IpII (Trafalgar Square) Tmax
IpII Tmax
IpII (Trafalgar Square) Tmin
IpII Tmin
Temperature (°C)
Age in Kyrs BP
20
15
10
5
0
-5
2
4
6
8
10
12
b)
Trafalgar Square
IpII - Deeping St James/Woolpack Farm/Tattershall Castle
FI II
Present Day
Tmax (ºC)
Tmin (ºC)
22
20
18
16
14
12
10
-3
-2
-1
0
1
2
3
4
5

Supplementary information 1

Table 1 – Proxy data taken, and updated, from Candy et al. (2010)

Thermophile	***Palaeoclimatic significance***
Trapa natans L.	Water chestnut is a floating annual aquatic plant that grows in slow-moving water. It is native to warm temperate parts of Eurasia and Africa and occurred in Britain during several interglacials, as well as during warmest part of the Holocene (Schofield and Bunting, 2005). *Trapa* is suggested to need several months of water temperatures over 20°C for fruiting (Meusel et al., 1978). Where present, *Trapa natans* is, therefore, used to infer summer temperatures of >/=20°C, although it is important to note that the ecological tolerances of this species are complex and in some settings, particularly at the edges of its range, its distribution may be in response to climatic variables other than temperature. Nevertheless, temperature thresholds for several key parts of its lifecycle have been recorded: general water temperatures of 12-15°C (Karg, 2006), temperatures above +16°C in order for seeds germination (Galanti et al., 1990) and above +20°C for flowering (Jorga et al., 1982) and for fruiting (Meusel et al., 1978). Since these last two are essential for the maintenance of successful populations, we apply the upper threshold of +20°C in this study. **MIS 5e sites: Trafalgar Square, Swanton Morley,** *Wortwell*
Salvinia natans (L.) All	*Salvinia natans* is the floating water-fern with a range focused in central and south-eastern Europe. This species is estimated to require water temperatures of 14-17 °C for germination (Wolff and Schwarzer, 2005). It is not naturalized in Britain today and its current western range extends to the Netherlands and Spain (Godwin, 1975). **MIS 5e sites: Bobbitshole**
Najas minor All.	The current range of this species, the brittle naiad, is central and eastern European range and British interglacial and Holocene occurrences therefore lie well outside its modern range. Its current most westerly occurrence is Belguim. Aalbersberg and Litt (1998) have suggested a minimum July temperature of 18 °C for its successful colonisation.

	MIS 5e sites: Trafalgar Square, Bobbitshole, Deeping St James
Acer monspessulanum L.	The Montpellier Maple prefers mild winters, 0°C and correspondingly warm summers, at least 17°C (Zagwijn, 1996). This species is no longer native to Britain and is currently restricted to the Mediterranean and central Europe (Godwin, 1975). **MIS 5e sites: Trafalgar Square, Woolpack Farm, Tattershall Castle, Bobbitshole**
Ilex aquifolium L. and *Hedera helix* L.	Both the Holly and ivy are frost intolerant plants and their current range does not extend far into eastern Europe (Godwin, 1975). Iversen (1944), has proposed that the lower thermal limit for January (mean temperature) for these two species are 0 °C and 1.5-2 °C, respectively. These limits only relate to these specific species. **MIS 5e sites: Trafalgar Square**
Cybister lateralimarginalis Geer	This water beetle species is commonly found in association with peat bogs or small lakes with dense vegetation at their margins (Nillson and Holmen, 1995). Although it is widespread in central and southern Europe it is occasionally found as north as the extreme south of Sweden and England. Such occurrences are uncommon and it appears unable to establish a permanent presence in these more northerly locations. **MIS 5e sites: Bobbitshole, Trafalgar Square, Deeping St James,** *Itteringham and Shropham*
Caccobius schreberi (L.)	A species of dung beetle that is commonly associated with the presence of large herbivorous mammals. It has not been recorded as living in Britain and its modern range is focussed in southern Europe and only in the warmer parts of central Europe. Harde (1984) records it as being more comer in the east of Europe with observed occurrences reaching as far west as the upper Rhine and Main basins. **MIS 5e sites: Bobbitshole, Trafalgar Square, Deeping St James, Woolpack Farm,** *Itteringham and Shropham*

Valgus hemipterus (L.)	This species is characteristic of modern day southern central Europe and is found as far north as the Netherlands. It is associated with rotting wood of a range of deciduous trees, within which its larvae develop. It is widespread in southern central Europe reaching as far north as The Netherlands. **MIS 5e sites: Bobbitshole, Trafalgar Square, Deeping St James, Tattershall Castle,** *Itteringham and Shropham*
Emys orbicularis (L.)	Extinct in Britain since the mid-Holocene (and only recorded at a single site in the current interglacial), the European pond tortoise is typically found in central, southern and eastern Europe where elevated summer temperatures aid successful incubation of its eggs (Stuart, 1979; Holman, 1998; Schneeweiß, 2004; Sommer et al., 2007). Temperature is, however, only one factor that controls its reproductive success with a complex set of synergistic factors being important, especially sunshine hours, soil temperature and moisture, as well as the availability of nesting sites. However, it is commonly suggested that a mean July temperature exceeding 17- 18^{o}C appears necessary for hatching success (Stuart, 1979). **MIS 5e sites: Bobbitshole, Swanton Morley,** *Itteringham and Shropham*
Temperate deciduous forest	Prentice et al. (1992) predicted temperatures that limited the development of specific ecosystem types. Temperate deciduous forest (dominated by temperate summergreen trees, cool-temperate conifers and boreal summergreen tree) is predicted to require Tmin temperatures between -2.5 and +5^{o}C to form. This is the ecosystem type of IpII, consequently, it is assumed that at any site where this occurs the absolute minimum value of Tmin must be -2.5^{o}C. **MIS 5e sites: Bobbitshole, Trafalgar Square, Deeping St James, Tattershall Castle, Woolpack Farm, Itteringham (?) and Shropham (?)**

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Supplementary information 2

Site	Sedimentology and Stratigraphy		Age attribution			Palaeoclimatic indicators									Combined temperatures		Key references
						Beetle MCR			Ostracod MOTR			Thermophile species					
	Depositional environment	*Pollen stage*	*AAR values*	*H. amphibius*	*Radiometric dating*	*Sample*	*Tmax*	*Tmin*	*Sample*	*Tmax*	*Tmin*	*Taxon*	*Tmax*	*Tmin*	*Tmax*	*Tmin*	
Trafalgar Square	Fluvial channel fill (Thames)	IpII	Val = 0.10 Ala = 0.19	+		43 species	17 to 21	-6 to 3	12 species	12 to 23	-1 to 5	*Trapa natans* *Najas minor* *Acer monspessulanum* *Helix hedera* *Deciduous woodland*	Tmax >/= 20 Tmax >/=18 Tmax >/=17	 Tmin >/=1.5 Tmin >/-2.5	**20 to 21**	**1.5 to 3**	Franks (1960) Candy et al. (2010) G.R. Coope unpublished data R.C. Preece unpublished data
Deeping St James	Fluvial channel fill (Welland)	IpIIb			OSL	44 species	17 to 18	-4 to 4				*Najas minor*	>/=18		**18**	**-2.5 to 4**	Keen et al. (1999)
Woolpack Farm, Fenstanton	Fluvial channel fill (Great Ouse)	IpII	Val = 0.09 Ala = 0.17			12 species	17 to 18	-4 to 4				*Acer monspessulanum*	>/=17				Gao et al. (2000)
Tattershall Castle	Fluvial channel fill (Witham)	IpIIb	Val = 0.09 Ala = 0.18			19 species	17 to 18	-4 to 4	16 species	16 to 22	-1 to 4	*Acer monspessulanum*	>/=17		**17 to 18**	**-1 to 4**	Girling (1974) Holyoak and Preece (1985)
Bobbitshole	Fluvio-lacustrine	IpII	Val = 0.10 Ala = 0.18			6 species	17 to 27	-7 to 9				*Salvinia natans* *Najas marina* *Najas minor* *Acer monspessulanum* *Emys orbicularis*	>/=14 >/=15 >/=18 >/=17 >/=18		**18 to 27**	**-2.5 to 9**	West (1957) Coope (1974) Stuart (1979)
Swanton Morley	Fluvial channel fill (Wensum)	IpIIa and IIb		+								*Trapa natans* *Emys orbicularis*	>/= 20 >/=18		**>/=20**	**?**	Stuart (1979) Coxon et al. (1980)
Itteringham	Fluvial-lacustrine (Bure)	?	Val = 0.09 Ala = 0.18			52 species	17 to 19	-5 to 1				*Emys orbicularis*	>/=18		**18 to 19**	**-5 to 1**	Hallock et al. (1990) G.R. Coope unpublished data
Shropham	Fluvial-lacustrine (Thet)	?	Val = 0.09 Ala = 0.18	+		43 species	17-18	-4 to 0				*Emys orbicularis*	>/=18		**18**	**-4 to 0**	Holman and Clayden (1990) Walkling (1996)

Supplementary information 3 – Beetle data

Species	Trafalgar Square	Deeping St James	Woolpack Farm	Tattershall Castle	Bobbitshole	Itteringham	
CARABIDAE							
Carabus granulatus L.		MCR					
Notiophilus aquaticus (L.)				MCR			
Notiophilus germinyi Fauvel	MCR		MCR				
Elaphrus cupreus Duft.		MCR		MCR		MCR	
Elaphrus riparius (L.)	MCR					MCR	
Clivina fossor (L.)		MCR					
Loricera pilicornis (F.)	MCR		MCR	MCR		MCR	
Nebria brevicollis (F.)			MCR				
Dyschirius aeneus (Dej.)		MCR		MCR			
Dyschirius globosus (Hbst.)	MCR	MCR		MCR		MCR	
Epaphius secalis (Payk.)	MCR	MCR				MCR	
Epaphius rivularis (Gyll.)						√	
Lasiotrechus discus (F.)		√					
Elaphropus parvulus (Dej.)		√					
Paratachys bistriatus (Duft.)	√						
Bembidion articulatum (Panz.)		√					
Bembidion assimile Gyll.	MCR	MCR		MCR	MCR	MCR	
Bembidion biguttatum (F.)		MCR					
Bembidion dentellum (Thun.)		√					
Bembidion doris (Panz.)		MCR	MCR			MCR	
Bembidion elongatum Dej.	√	√				√	
Bembidion fumigatum (Duft.)						MCR	
Bembidion gilvipes Sturm		MCR		MCR			
Bembidion guttula (F.)	MCR			MCR			
Bembidion iricolor Bedel				√			
Bembidion lampros (Hbst.)		MCR					
Bembidion lunulatum (Fourc.)			√				
Bembidion mannerheimi Sahl.	MCR	MCR					
Bembidion obtusum Serv.	MCR	MCR	MCR				
Bembidion octomaculatum (Goeze)	MCR	MCR		MCR		MCR	
Bembidion properans (Steph.)	MCR		MCR				
Bembidion punctulatum Drap.			MCR				
Bembidion quadrimaculatum (L.)	MCR	MCR	MCR			MCR	
Bembidion quadripustulatum Serv.		MCR					
Bembidion transparens (Gebler)							
Bembidion varium (Ol.)	MCR	MCR					
Asaphidion flavipes (L.)		MCR					
Patrobus atrorufus (Ström.)						MCR	
Bradycellus ruficollis (Steph.)						MCR	
Poecilus lepidus (Lesk.)			MCR				

Pterostichus anthracinus (Ill.)		√				√
Pterostichus aterrimus (Hbst.)						
Pterostichus diligens (Sturm						MCR
Pterostichus gracilis (Dej.)	MCR	MCR				
Pterostichus melanarius (Ill.)		MCR		MCR		
Pterostichus minor (Gyll.)		MCR		MCR		MCR
Pterostichus niger (Schall.)	MCR		MCR			
Pterostichus nigrita (Payk.)	MCR	MCR				MCR
Pterostichus strenuus (Panz.)	MCR	MCR				MCR
Pterostichus vernalis (Panz.)	MCR	MCR			MCR	MCR
Calathus fuscipes (Goeze)	MCR		MCR			
Calathus melanocephalus (L.)						MCR
Platynus livens (Gyll.)	MCR					
Agonum thoreyi Dej.						MCR
Agonum viduum (Panz.)		MCR				MCR
Paranchus albipes (F.)	MCR			MCR		
Oxypselaphus obscurus (Hbst.)		MCR				
Amara ovata (F.)						
Zabrus tenebrioides (Goeze)	MCR		MCR		MCR	
Chlaenius festivus (Panz.)	√					
Chlaenius nigricornis (F.)				MCR		MCR
Chlaenius quadrisulcatus (Payk.)		√				
Chlaenius sulcicollis (Payk.)	MCR					MCR
Chlaenius tristis (Schall.)	√					√
Chlaenius variegatus (Geoff.)	MCR					
Oodes gracilis Villa & Villa	MCR	MCR		MCR	MCR	MCR
Oodes helopioides (F.)	MCR	MCR		MCR	MCR	MCR
Badister bullatus (Schrank)				MCR		
Badister unipustulatus Bond.						MCR
Panagaeus cruxmajor (L.)	MCR					MCR
Odacantha melanura (L.)	MCR	MCR		MCR	MCR	MCR
Dromius quadrimaculatus (L.)		√				
Syntomus foveatus (Geoff.)	MCR					
Polystichus connexus (Geoff.)		MCR				
DYTISCIDAE						
Hydrovatus clypealis Sharp						√
Hygrotus inaequalis (F.)		MCR				
Hygrotus impressopunctatus (Schall.)						MCR
Bidessus minutissimus (Germ.)				√		
Hydroporus palustris (L.)				MCR		
Nebrioporus depressus (F.)	√					
Platambus maculatus (L.)	MCR					
Copelatus haemorrhoidalis (F.)		MCR				
Agabus bipustulatus (L.)	MCR	MCR	MCR	MCR		MCR
Agabus nebulosus (Forst.)				MCR		

Agabus sturmii (Gyll.)						√
Colymbetes fuscus (L.)		MCR				
Cybister lateralimarginalis (Deg.)		√				√
GYRINIDAE						
Gyrinus substriatus Steph.	√	√				
Gyrinus suffriani Scriba	MCR	MCR			MCR	MCR
Orectochilus villosus (Müll.)	√	√				√
RHYSODIDAE						
Rhysodes sulcatus (F.)		√				
HYDROPHILIDAE						
Ochthebius bicolon Germ.				MCR		
Ochthebius minimus (F.)		MCR				MCR
Hydraena riparia Kug.				MCR		MCR
Hydrochus angustatus Germ.		√				
Helophorus aequalis Thoms.		√				
Helophorus brevipalpis Bedel				√		
Helophorus grandis Ill.				MCR		
Hydrophilus piceus (L.)						
Coelostoma orbiculare (F.)	MCR	MCR	MCR	MCR	MCR	MCR
Sphaeridium bipustulatum F.	√	√	√			
Cercyon convexiusculus Steph.	√			√		√
Cercyon marinus Thoms.	√					
Cercyon melanocephalus (L.)						√
Cercyon pygmaeus (Ill.)	√		√			
Cercyon sternalis Sharp		√				√
Cercyon tristis (Ill.)						MCR
Cercyon ustulatus (Preys.)						√
Megasternum obscurum (Marsham)		MCR	MCR	MCR		MCR
Cryptopleurum crenatum (Panz.)	√					
Cryptopleurum minutum (F.)		√				√
Hydrobius fuscipes (L.)	MCR	MCR		MCR		MCR
Limnoxenus niger (Zsch.)	√	√				√
Chaetarthria seminulum (Hbst.)	MCR	MCR	MCR	MCR		MCR
Hydrochara caraboides (L.)		√				√
Hydrophilus piceus (L.)		√				√
Berosus luridus (L.)	MCR	MCR				MCR
HISTERIDAE						
Onthophilus striatus (Müll.)		√				√
Phosphuga atrata (L.)		√		√		√
Corylophus crassidoides (Marsham)		√				
STAPHYLINIDAE						
Micropeplus porcatus (F.)		√				√
Micropeplus staphylinoides (Marsham)		√		√		
Olophrum piceum (Gyll.)	MCR	MCR	MCR			MCR
Acidota cruentata Mann.						MCR

Acrolocha sulcula (Steph.)			√			
Lesteva longoelytrata (Goeze)						MCR
Lesteva punctata Er.				MCR		MCR
Anotylus rugosus (F.)		MCR		MCR		MCR
Oxytelus piceus (L.)			MCR			
Oxytelus sculptus Grav.	√					
Platystethus arenarius (Geoff.)		MCR		MCR		
Platystethus cornutus (Grav.)	√		√			√
Platystethus nitens (Sahl.)		MCR		MCR		MCR
Platystethus nodifrons Mann.		MCR	MCR			
Stenus biguttatus (L.)						
Stenus juno (Payk.)						MCR
Rugilus fragilis (Grav.)				MCR		
Euaesthetus laeviusculus Mann.		MCR				
Tachyporus chrysomelinus (L.)		√				
Tachinus lignorum (L.)	MCR					
Tachinus rufipes (L.)						
Drusilla canaliculata (F.)				MCR		
Trichonyx sulcicollis (Reich.)		√				
Reichenbachia juncorum Leach		√				
DRYOPIDAE						
Pomatinus substriatus (Müll.)		√	√			
Stenelmis canaliculata (Gyll.)		√				
Elmis aenea (P. Müller)		√				√
Esolus parallelepipedus (P. Müller)		√		√		√
Oulimnius tuberculatus (P. Müller)		√				√
Oulimnius troglodytes (Gyll.)		√				
Limnius volckmari (Panz.)		√				
Normandia nitens (P. Müller)		√		√		
Macronychus quadrituberculatus P. Müller		√		√		
SCARABAEIDAE						
Copris lunaris (L.)	MCR		MCR	MCR		MCR
Caccobius schreberi (L.)	MCR	MCR			MCR	MCR
Onthophagus coenobita (Hbst.)				√		
Onthophagus furcatus (F.)		√	√			√
Onthophagus gibbulus (Pallas)	MCR					
Onthophagus massai Baraud	√	√				√
Onthophagus taurus (Schreb.)	MCR	MCR			MCR	
Onthophagus vacca (L.)	√		MCR	MCR		
Onthophagus verticicornis (Laich.)		√	√			
Aphodius carpetanus Graëlls			√			
Aphodius consputus Creutz.		√				
Aphodius depressus (Kug.)						
Aphodius erraticus (L.)			MCR			
Aphodius fimetarius (L.)						

Aphodius fossor (L.)	MCR	MCR	MCR
Aphodius porcus (F.)		√	
Aphodius rufipes (L.)		MCR	MCR

NB: MCR = used in MCR calculation, √ = present but no associated MCR data

Supplementary information 3 – Ostracod data

Trafalgar Square

Unpublished data (RCP)

- *Candona candida* (O.F. Müller)*
- *Candona neglecta* Sars*
- *Candona rostrata* Brady & Norman
- *Candona sp.*
- *Cyclocypris laevis* (Müller)*
- *Cyprideis torosa* (Jones)
- *Cypridopsis vidua* (O.F. Müller)*
- *Darwinula stevensoni* (Brady & Robertson)*
- *Herpetocypris chevreuxi* (Sars)*
- *Herpetocypris sp.*
- *Heterocypris salina* (Brady)*
- *Ilyocypris bradyi* (Sars)
- *Ilyocypris gibba* Ramdohr
- *Limnocythere inopinata* (Baird)*
- *Potamocypris arcuata* (Sars)*
- *Potamocypris zschokkei* (Kaufmann)*
- *Prionocypris zenkeri* (Norman)*
- *Pseudocandona hartwigi* (G.W. Müller)*
- *Psychodromus olivaceus* (Brady & Norman)*

Tattershall Castle

Holyoak & Preece (1985)

- *Candona angulata* G.W. Müller*
- *Candona candida* (O.F. Müller)*
- *Candona* cf. *levanderi* Hirschmann
- *Candona neglecta* Sars*
- *Candona* sp.
- *Cyprideis torosa* (Jones)
- *Cypridopsis vidua* (O.F. Müller)*
- *Darwinula stevensoni* (Brady & Robertson)*
- *Eucypris pigra* (Fischer)*
- *Eucypris* sp.
- *Herpetocypris brevicaudata* Kaufmann*
- *Herpetocypris chevreuxi* (Sars)*
- *Herpetocypris reptans* (Baird)*
- *Herpetocypris* sp.
- *Heterocypris salina* (Brady)*
- *Ilyocypris bradyi* (Sars)
- *Nannocandona* sp.
- *Notodromas monacha* (O.F. Müller)*
- *Prionocypris zenkeri* (Norman)*
- *Prionocypris* sp.
- *Pseudocandona compressa* (Koch)*
- *Pseudocandona pratensis* (Hartwig)*
- *Scottia pseudobrowniana* Kempf*